Life history constrains biochemical development in the highly specialized odontocete echolocation system

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The vertebrate head has undergone enormous modification from the features borne by early ancestors. The growth of skull bones has been well studied in many species, yet little is known about corresponding soft tissue development. Among mammals, some of the most unusual examples of cranial evolution exist in the toothed whales (odontocetes). Specialized fat bodies in toothed whale heads play important roles in sound transmission and reception. These fat bodies contain unique endogenous lipids, with favourable acoustic properties, arranged in highly organized, three-dimensional patterns. We link variation in developmental rates of acoustic fats with life-history strategy, using bottlenose dolphins and harbour porpoises. Porpoise acoustic fats attain adult configurations earlier (less than 1 year) and at a faster pace than dolphins. The accelerated lipid accumulation in porpoises reflects the earlier need for fully functional echolocation systems. Dolphins enjoy 3–6 years of maternal care; porpoises must achieve total independence by approximately nine months. Further, a stereotypic 'blueprint' for the spatial distribution of lipids is established prior to birth, demonstrating the highly conserved nature of the intricate biochemical arrangement in acoustic tissues. This system illustrates an unusual case of soft tissue development being constrained by life history, rather than the more commonly observed mechanistic or phyletic constraints.

Keywords: development; ontogeny; vertebrate life history; dolphin; porpoise

1. INTRODUCTION

The heads of vertebrates are recognized as being potentially the most disparate body parts, with changes in cranial structure being fundamental to adaptation (Hanken & Gross 2005). Among mammals, a diverse array of skeletal and soft tissue alterations reflect specialized adaptations for feeding, breathing, sensory perception, sexual selection and defence. Development of the head is recognized as being particularly complex, as multiple organ systems must change and grow simultaneously (Thomson 1988; Kuritani *et al.* 1997). Although the head has been well studied in terms of anatomy, morphology and function (e.g. Trainor 2003; Helms *et al.* 2005; Olsson *et al.* 2005), we have little knowledge about how its growth is controlled (Thomson 1988). Although patterns of growth in the osteological components of vertebrates have been investigated in many species (Moore 1981; Hanken & Hall 1993), far less attention has been paid to factors influencing development in corresponding soft tissues.

Toothed whales (Cetacea: Odontoceti) exhibit extreme morphological and physiological alterations to the typical mammalian body plan. Adaptations for echolocation include reorganization and reshaping of skull features, modifications to ear bones and development of specialized acoustic fat bodies (Norris 1968; Fordyce 2002). The

melon (in the forehead) and mandibular fats (in and around the lower jaws) are assumed to play roles in transmission and reception, respectively, of sound (Norris 1968; Morris 1986). The 'acoustic' tissues are composed primarily of suites of short- and branched-chain fatty acids (FA) not found in adipose tissues of other mammals (Litchfield *et al.* 1975; Malins &Varanasi 1975). In most vertebrates, the lipid composition of adipose tissue reflects input from both dietary and endogenous sources, with the dominant source depending on many factors, including age class, nutritional status and seasonal foraging patterns (Pond 1998). In mammals, endogenous lipid synthesis coupled with subsequent elongation and desaturation processes result in four FA (16 : 0, 16 : 1, 18 : 0 and 18 : 1) being most prevalent in the biosynthetic pool (e.g. Mead *et al.* 1986; Iverson 1993; Pond 1998). Even specialized adipose depots, such as the humps of camels or foot pads of bears, are dominated by these four components (e.g. Pond *et al.* 1992; Kadim *et al.* 2002).

In addition to their chemical structures being unusual, the FA in odontocetes are distributed in complex, non-random three-dimensional patterns in acoustic fat bodies, often forming a core inside shells of longer, straight-chain FA. As odontocete cranial FA exhibit different acoustic properties unlike those of the longer-chain FA typically found in mammalian adipose (Gouw & Vlugter 1967; Hustad *et al.* 1971), this arrangement serves to channel sound waves through the fats, and is considered extremely important to tissue function (Litchfield *et al.* 1973; Varanasi *et al.* 1975, 1982). Interestingly, even within

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this modification of mammalian physiology to synthesize short- and branched-chain lipids, there is considerable interfamily variation. Acoustic fats of ziphiids, for example, are dominated by isolauric (i-12 : 0) acid (Koopman *et al.* 2006). In delphinids, phocoenids and monodontids, the main branched-chain FA in acoustic tissues are isovaleric (i-5 : 0) and isopentadecanoic (i-15 : 0) acids (Litchfield *et al.* 1975; Koopman *et al.* 2006). Rather than being produced via the sequential addition of two-carbon units in the liver, these FA are believed to be synthesized as intermediates in amino acid degradation (Morii & Kaneda 1982). i-5 : 0 is highly toxic to other mammals (Wretlind 1957; Tanaka *et al.* 1966), and in fact the only mammals in which this molecule is known to accumulate are human patients suffering from isovaleric acidemia, a heritable disease that can be fatal (Tanaka *et al.* 1966). Yet in some odontocete acoustic fats, i-5 : 0 can comprise more than two-thirds of all FA present (Koopman *et al.* 2003, 2006).

Although we have recognized for almost half a century that toothed whales produce unusual lipids for echolocation, the rates of acquisition of functionally meaningful concentrations of these FA in the acoustic fat bodies have never been closely examined. Typically, the growth of mammalian adipose tissues is characterized by rapid proliferation of cells early in life, with increases in cell size accounting for changes in adipose depot variation thereafter (Pond 1984, 1998). The biochemical composition of a given depot generally reflects diet and normal biosynthesis throughout life. In young mammals, adipose tissue composition is usually a direct reflection of maternal milk lipids (e.g. Garton & Duncan 1969; Lodge *et al.* 1978; Pond 1998). Clearly, this is not the case for the odontocete acoustic fats: the milk of toothed whales, like that of all other mammals, is composed mostly of lipids of dietary and more typical biosynthetic origin, and does not contain any branched-chain FA (Iverson & Oftedal 1995; Koopman *et al.* 2003).

We compared rates of biochemical development in two species of odontocetes, bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*). These animals were selected for two reasons. First, the acoustic tissues of both species contain similar unusual FA (namely i-5 : 0 and i-15 : 0; Litchfield *et al.* 1973; Gardner & Varanasi 2003; Koopman *et al.* 2003, 2006). Second, these species exhibit very different life-history strategies in terms of parental care. *Tursiops* calves remain with their mothers, and do not become independent, until they are between 3 and 6 years of age, after which they are termed subadults (Wells & Scott 1999; Wells 2003). *Phocoena* calves, on the other hand, must achieve full independence incredibly rapidly, being able to survive on their own within 9–10 months (Read & Hohn 1995; Read 1999). If one accepts that high concentrations of branched-chain FA in the acoustic fats are necessary for proper tissue function, one would hypothesize that dolphin calves would display protracted development of those tissues (over years), and that mature acoustic fat bodies would not be required until animals are completely independent (subadults and older). Young porpoises, on the other hand, need to be able to carry out all activities associated with echolocation (foraging, predator avoidance, socialization) within months and therefore require fully functional sound transmission and

reception systems. Thus acoustic lipid levels and composition in porpoise calves would be expected to approach those of adults much more quickly.

2. MATERIAL AND METHODS

Acoustic fat samples were collected from the mandibular fat bodies of 12 bottlenose dolphins and 10 harbour porpoises that had been either stranded, or had been killed incidentally in commercial fishing operations, along the Atlantic coast of Canada and the United States. Specimens ranged in age class from foetus to adult, defined using standard criteria (Read & Hohn 1995; Wells & Scott 1999). Necropsies were carried out using standard protocols, and all tissues were considered to be fresh, with samples either being collected, or the specimen being frozen for later thawing and dissection, within 24 hours of death (Geraci & Lounsbury 1993; McLellan *et al.* 2002). All animals were classified as being in excellent body condition, exhibiting none of the classic signs of emaciation (Geraci & Lounsbury 1993; Kastelein & van Battum 1990). Lipids were extracted, separated and analysed for FA content as butyl esters by gas chromatography (see Koopman *et al.* (2003, 2006) for specific details). Because the wax content in porpoise tissues is relatively low (less than 7%; Koopman *et al.* 2006), we report only the triacylglycerol composition here. For interspecific comparisons of ontogeny, samples from the fat body found inside the mandibular fossa, at a position known to contain high concentrations of branched-chain FA (Koopman *et al.* 2006), were used to standardize sample location. An additional sample of melon from a 53-cm foetal porpoise was included. This was justifiable for two reasons: first, ontogenetic accumulation of branched-chain FA in the melons of porpoises shows patterns very similar to those observed for mandibular fats (Koopman *et al.* 2003); second, within a given individual, concentrations of i-5 : 0 in melon and mandibular fats are highly correlated, regardless of species or age class (H. N. Koopman 2006, unpublished data).

Because the dolphins showed slower development of acoustic lipid composition than the porpoises, with a wider range of values across age classes, they were a better candidate species in which to explore the existence of a set, spatial, biochemical distribution pattern. To evaluate ontogeny in the three-dimensional patterns of FA distribution in dolphins, approximately fifty 0.5-g subsamples were collected from each of 10 heads as described previously (Koopman *et al.* 2006), sampling the fat body lying inside the fossa ('inner fat'), the fat situated superficial to the pan bone ('outer fat') and the cranial blubber overlying the entire mandibular region ('cranial blubber'), and analysed as above (see figure 1). For each specimen, mandibular fat bodies were divided into transverse slices (numbered 1 (posteriorly) through to 5 (anteriorly)), and a number of subsamples (numbered 1 dorsally through to 4 ventrally) were obtained from each tissue component (i.e. inner, outer or blubber) of each slice.

FA data are calculated as wt% of total FA present and are therefore highly correlative, limiting the potential for rigorous statistical analyses, particularly on such a small dataset. It was possible to test for a significant pattern in the spatial distribution of FA in *Tursiops* mandibular fats using non-parametric statistics, which are not constrained by the same assumptions as parametric approaches, and are highly efficient for small sample sizes (Steel & Torrie 1980). Analyses were limited to cranial blubber only to reduce the chance of making type I errors. To determine whether there
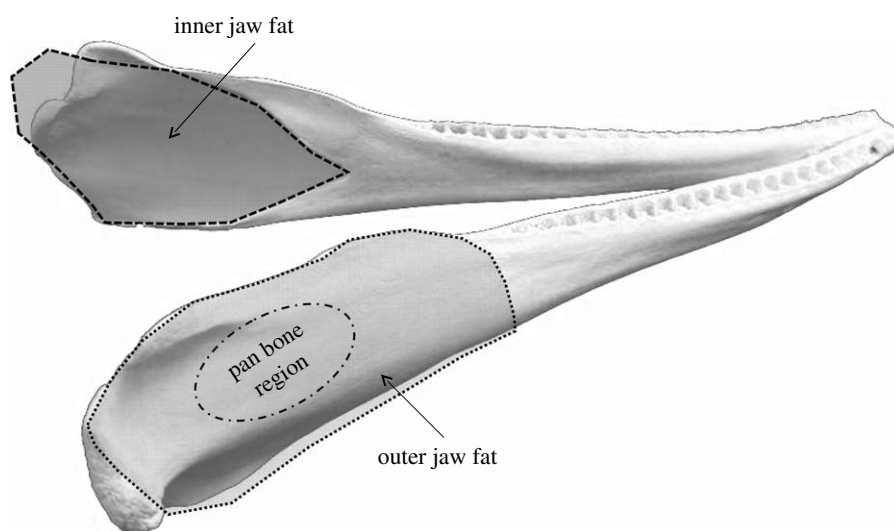
Figure 1. Schematic depicting locations of inner and outer jaw fats, overlaid onto the mandible of a bottlenose dolphin. Note that the cranial blubber (not shown) lies over, and superficial to, the outer jaw fat; also note the location of the pan bone.

were specific areas with relatively high concentrations of acoustic FA, each sample site within each slice was ranked according to its total branched-chain FA content, separately for each individual. Analysis of variance (ANOVA) on ranked data was used to determine the presence of spatial patterns; this method is equivalent to a Kruskal–Wallis test but permits inclusion of more than one factor. Dolphins were divided into three age classes as follows: adult, subadult and calf/foetus (see above); factors tested were age class, slice and sample site. The initial ANOVA revealed significant slice×sample site interaction ($p < 0.001$); thus the analysis was repeated separately for each slice. Differences among sample sites were further evaluated using *post hoc* Bonferroni (error variances equal) or Tamhane's T2 (error variances not equal). All statistics were calculated using SPSS v. 15.0 (SPSS Inc., Chicago, IL).

3. RESULTS

Seventy different FA were identified in the mandibular fats. Samples were dominated by short- and branched-chain compounds (not found in typical mammalian adipose (Pond 1998)), as well as saturated and monounsaturated FA, but unlike blubber (Koopman 2007), polyunsaturated FA were virtually absent. Concentrations of total branched-chain FA in jaw fats increased with body size in both species. *Tursiops* calves showed intermediate values (27.8–46.5 wt%) to those of the foetus (9.2 wt%) and subadults (64.4–73.4 wt%), and were below adult values (74.0–80.0 wt%; figure 2a). However in *Phocoena* calves, total branched-chain concentrations (24.6–46.1 wt%) were similar to those of subadults (31.3–48.5 wt%) and adults (40.1–48.0 wt%; figure 2b). Restricting the analysis to the single most dominant FA (*i*-5 : 0) (figure 3) revealed that porpoises reach adult accumulations relatively quickly, in an almost linear fashion, while dolphins exhibit a more typical allometric relationship that takes longer (in terms of growth) to maximize.

All three mandibular fat bodies (inner fat, outer fat and cranial blubber) of adult dolphins showed spatial heterogeneity in lipid composition. In some cases, specific regions of the mandibular fats contained concentrations of branched-chain FA up to 10-fold higher than samples
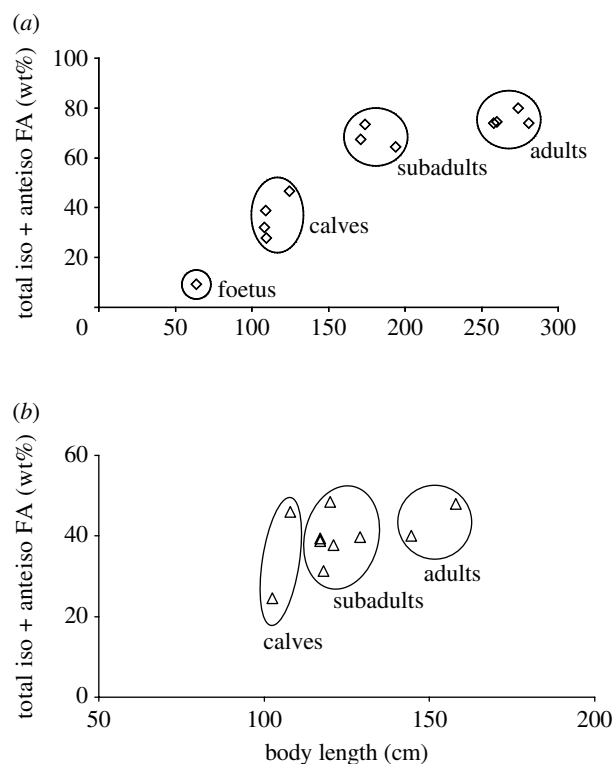

Figure 2. Concentrations (wt% of all FA present) of total iso (*i*-) and anteiso (*ai*-) acids as a function of body size. (a) Bottlenose dolphins (*T. truncatus*) ($n = 12$), (b) harbour porpoises (*P. phocoena*) ($n = 10$). Age classes are shown in ovals for each species. Total *i*- and *ai*- acid values were calculated by summing the wt% of *i*-4 : 0, *i*-5 : 0, *i*-11 : 0, *ai*-11 : 0, *i*-12 : 0, *i*-13 : 0, *ai*-13 : 0, *i*-14 : 0, *i*-15 : 0, *ai*-15 : 0, *i*-16 : 0 and *i*-17 : 0. Corresponding approximate ages for dolphin age classes are as follows: calves 1–3 years, subadults approximately 4–6 years, adults more than 6 years (Wells & Scott 1999); for porpoises, calves 3–9 months, subadults 1–3 years, adults more than 3 years (Read & Hohn 1995; Read 1999).

collected only a few centimetres away; these patterns were consistent across individuals (e.g. figure 4). ANOVA of ranked data from cranial blubber (see figure 4 for orientation) showed no significant age class effects (all $p > 0.30$), and no significant age class×sample site
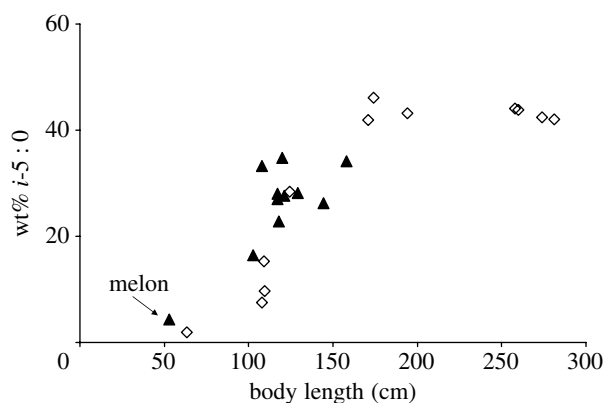
Figure 3. Concentrations (wt% of all FA present) of i-5 : 0 acid as a function of body size in bottlenose dolphins (*T. truncatus*; diamonds) ($n = 12$) and harbour porpoises (*P. phocoena*; triangles) ($n = 10$). Note that data from a sample of foetal melon have been added as a proxy for jaw fats for porpoises.

interaction (all $p > 0.08$), in any of the five slices. In addition, there was no significant sample site effect in slice 1 ($p > 0.13$). However, the other four slices (2 through to 5) all showed significant differences across sample sites (all $p < 0.001$). In slices 2, 3 and 4, sample site 2 consistently showed the highest levels of total branched-chain FA in all specimens (all $p < 0.018$). In slice 5, site 1 had the highest values ($p < 0.001$). In all the slices, site 4 (the ventral-most site) exhibited the lowest levels of acoustic FA (see figure 4).

4. DISCUSSION

According to Seilacher (who pioneered the concept of constructional morphology in 1970) and later Thomson (1988), body systems develop under a series of limitations, including structure–function, cell mechanics and phyletic constraints. Here we present an example of development proceeding according to constraints imposed by life-history strategy. In young mammals, growth of mammalian adipose tissue is typically characterized by changes in cell number, and later on cell size, rather than composition (Pond 1984, 1998; Kadim *et al.* 2002). Composition itself is regulated by a combination of diet and normal biosynthetic pathways, dependent upon a given animal's energy balance and growth needs. Even among unusual and extremely specialized adipose depots, changes in lipid composition parallel those of the rest of the body's adipose tissues (Pond *et al.* 1992; Kadim *et al.* 2002). With their atypical FA profiles, which differ from those of the blubber (Koopman 2007), toothed whale acoustic tissues represent a significant departure from normal mammalian physiology.

We propose that the differential rates of attaining adult concentrations of branched-chain, acoustic FA in these two species are directly tied to their life-history characteristics. Bottlenose dolphins nurse for 12–18 months and calves enjoy extended maternal care for 3–6 years, being dependent on their mothers for socialization, navigation, protection from predators, acquiring prey and occasional nutritional boosts from milk (Wells & Scott 1999; Wells 2003). In contrast, harbour porpoise calves undergo accelerated development, beginning to take solid food at approximately four months of age and becoming

entirely independent between 9 and 10 months of age (Smith & Read 1992; Read & Hohn 1995). For porpoises, physiological development must occur very rapidly if young animals are to survive on their own, as there is no maternal care or protection offered after the first year.

Ontogenetic changes in bottlenose dolphin acoustic tissues exhibited an interesting and direct parallel with the physiological maturation of muscle oxygen carrying capacity associated with the development of diving ability in this species. On average, the branched-chain FA complement in acoustic tissues of harbour porpoise calves was 80% that of adult conspecifics; in *Tursiops* calves this fraction was roughly half (48%). Average myoglobin (Mb) levels in locomotor muscles of juvenile (138–191 cm) *Tursiops* are 57% of adult values (Noren *et al.* 2001), remarkably close to the relative developmental state of the acoustic fat bodies. Thus multiple aspects of physiological development appear to be temporally coupled in dolphins. The ontogeny of Mb levels in *Phocoena* has not yet been established; thus we cannot evaluate whether acoustic and diving developments correspond in porpoises as well.

A novel discovery was the establishment of clear, common patterns of FA distribution at very early stages in the development of *Tursiops* (figure 4). Differences between adjacent samples were most dramatic in cranial blubber, where very high levels of acoustic FA were found in the tissue overlying the pan bone (figures 1 and 4). This is (coincidentally) the location of Norris' 'acoustic window' (Norris 1968), a region through which sound is believed to enter the head, and the location of greatest acoustic sensitivity in bottlenose dolphins (Brill & Harder 1991; Møhl *et al.* 1999). In cranial blubber, the stereotypical spatial patterns of acoustic FA accumulation were evident even in the foetus (figure 4). We interpret the strong sample site effect in slices 2–5 as evidence of a set, heterogeneous pattern of branched-chain FA distribution in these portions of the acoustic tissue. The key is the lack of an age class effect, which indicates that this *relative* pattern (i.e. spatial locations where levels of branched-chain FA are the highest and lowest within an individual) holds across the entire ontogenetic series. Thus biochemical development of the entire acoustic reception apparatus proceeds according to a pre-determined blueprint. The existence of an acoustic lipid *bauplan* is supported by previous anecdotal observations of a young Sowerby's beaked whale (*Mesoplodon bidens*; Koopman *et al.* 2006) and a sperm whale calf (*Physeter macrocephalus*; Morris 1975) exhibiting similar spatial distributions of unusual endogenous lipids in cranial acoustic tissues as adult conspecifics.

The consistent and early appearance of this arrangement of lipids indicates that the enzymatic machinery regulating formation of i- and ai- acids is (i) activated *in utero* and (ii) under very fine-scale spatial control to produce such high variation in relative concentrations of FA across small tissue distances. All evidence regarding synthesis of i-5 : 0 and other branched-chain FA in odontocetes points to isolated and localized production in adipose tissues (i.e. not formed in the liver and transported, but synthesized *in situ*; Malins & Varanasi 1975; Morii & Kaneda 1982; Koopman *et al.* 2003). Unlike blubber, lipids in acoustic tissues are metabolically immune to mobilization during periods of fasting
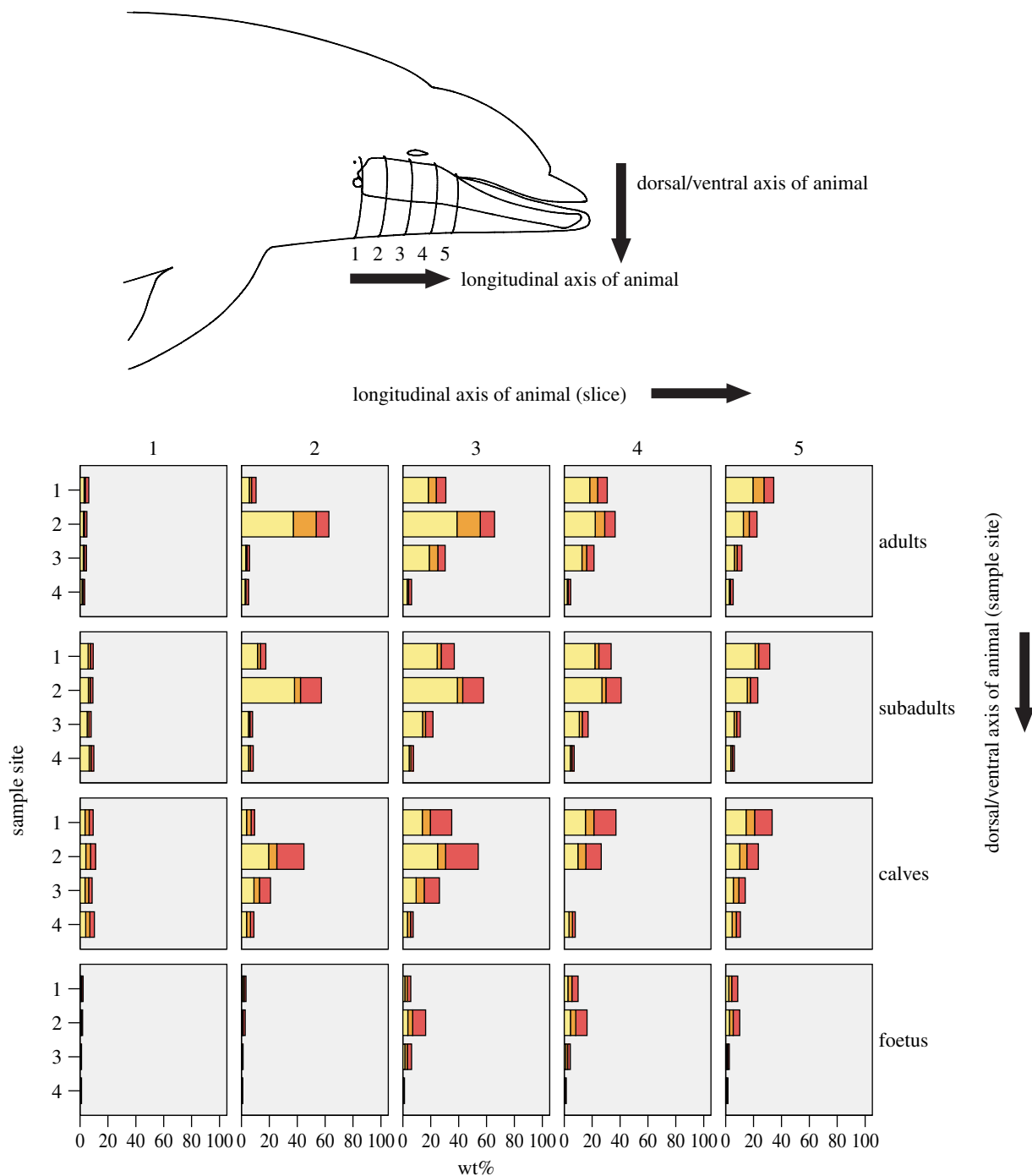
Figure 4. Spatial and ontogenetic variations in FA composition of acoustic tissues in bottlenose dolphins (*T. truncatus*; adults $n=4$, subadults $n=3$, calves $n=2$, foetus $n=1$). Coloured bars represent contributions of two *i*-acids (*i*-5 : 0 (yellow) and *i*-15 : 0 (orange)), and all other *i*- and *ai*-acids (red), to the total FA composition as wt%. Shown here are data from the cranial blubber; patterns in inner and outer mandibular fat bodies were similar. Vertical slices of tissue run from 1 caudally to 5 cranially; sample site runs from 1 dorsally to 4 ventrally. Establishment of regions of relatively high concentrations of branched-chain acids is evident as early as in the foetal stage; we argue this represents a 'blueprint' for acoustic lipid deposition patterns. Dolphin head image courtesy S. A. Rommel, UNCW.

(consequently not affected by health or nutritional status; Cranford *et al*. 1996; Koopman *et al*. 2002, 2003), thus very little de novo branched-chain FA synthesis should be required by adults. Although foetal values of *i*-5 : 0 were similarly low in both species (less than 5 wt%; figure 3), these levels serve to demonstrate that mechanisms controlling branched-chain FA synthesis are triggered prior to birth. The activation of such a specific FA synthetic pathway *in utero* is unusual, as mammalian foetuses typically contain very little adipose tissue (Pond

1984, 1998); any adipose that is present contains primarily those FA that are the physiological endpoints of normal biosynthesis. Over 80% of the adipose tissues of both neonatal calves (*Bos taurus*) and lambs (*Ovis domesticus*), for example, consists of 16 : 0 and 18 : 1 (Garton & Duncan 1969, 2002). Adipose tissue develops rapidly post parturition, particularly during the nursing period (Pond 1998). Given these and previous data (Gardner & Varanasi 2003), we hypothesize that in toothed whales, rates of branched-chain FA synthesis must be slow in

initial stages of embryonic and foetal development, become upregulated peri- and post parturition and potentially decline as animals reach adulthood. The post-parturition portion of i-5 : 0 synthesis (and potentially of the other branched-chain FA as well) appears to be constrained by the developmental timeline imposed by the life-history characteristics of a given species.

The logical question arising from this study is to ask whether these biochemical findings translate into functional significance. Unfortunately, there are few studies on the behavioural aspects of the ontogeny of echolocation in toothed whales, and thus evaluation of the potential functional consequences of our observations must be very limited. In addition, the majority of the data that do exist describe only sound production, not reception/perception. Young members of some species may not have fully functional echolocation systems: clicks produced by neonatal sperm whales are very different from those of adults and cannot be used for biosonar, though they might serve as communication signals (Madsen *et al.* 2003). Studies of captive odontocetes suggest that development and mastery of echolocation are probably a combination of physiological development and learning. Dolphin calves begin producing echolocation clicks at 22 days post partum; the first two months are recognized as being important in the development of echolocation ability, with significant influence from the mother's acoustic behaviour (Kuczaj 2004; Tranel & Kuczaj 2005). Finless porpoises (*Neophocoena phocaenoides*) have also been recorded making click trains as early as 22 days post partum (Li *et al.* 2007). Thus dolphins and porpoises are clearly able to produce high-frequency sounds at early stages of life, but the relative hearing capabilities of these young animals are unknown. The other group of echolocating mammals (bats) has functional binaural hearing by 25 days post partum (Razak & Fusessery 2007); however the sound reception mechanisms used by bats are completely different from those of odontocetes, making it difficult to generalize across echolocators.

Although sound production has been studied across many odontocetes, hearing has only been tested in a dozen species, with few direct measures of hearing having been made on extremely young animals. Nachtigall *et al.* (2005) found an infant Risso's dolphin (*Grampus griseus*) to exhibit greater sensitivity to high frequency sound than the only adult *G. griseus* to have been tested. However, there are probably considerable individual differences in high-frequency hearing (Ridgway & Carder 1997), confounding the ability to draw conclusions about the relative hearing capabilities of young dolphins. All of the available evidence points to young toothed whales possessing some ability to produce and receive high-frequency sounds associated with echolocation, but the comparative performance, sensitivity and fine-tuning of the acoustic systems of young animals relative to those of older individuals, and the precise point in time at which this system is fully mature, have not yet been elucidated. This makes interpretation of our dataset in a functional sense extremely difficult.

Do porpoises experience accelerated acoustic development because their acoustic fats reach the adult complement more rapidly than do those of dolphins? Without an ontogenetic series of hearing measurements from each species, we cannot yet answer this question. Taken together, the spatial placement, rates of accumulation and mode of synthesis of these acoustic lipids, in conjunction with their physiological peculiarities, provide a convincing case for a highly specialized system with carefully controlled development. Two recent studies on striped dolphins (*Stenella coeruleoalba*; Scano *et al.* 2005; Maxia *et al.* 2007) offer further support for the ontogenetic maturation of acoustic fats from a histological perspective; these authors showed that in addition to biochemical accumulation, the melon and jaw fats also undergo morphological changes with age, and they too suggested that this process would result in different sound reception properties. The presence and arrangement of the unusual acoustic lipids also offer a fairly compelling argument from a functional perspective, as completion of acoustic fat development is timed to coincide with independence. It is odd enough that i-5 : 0 and the other branched-chain FA are present in such high quantities in the heads of odontocetes, but what we have now demonstrated, for the first time, is that the development of these incredible adipose depots does not proceed uniformly across species. Is this an example of heterochrony in mammalian physiology? Zeldicth (2003) broadly defines heterochrony as 'an evolutionary change in developmental timing', which could certainly be argued here, although perhaps on a much finer scale than the manner which the term is normally used (Thomson 1988).

Not only have dolphins and porpoises made a major departure from typical mammalian physiology by accumulating these FA in their acoustic tissues, they have further modified the unusual synthetic process for these molecules by altering the rates at which the adult state is attained. Among mammals, there are numerous examples of physiology constraining life history. The extremely low size of bear cubs at birth, for example, represents an energetic adaptation to spare maternal protein stores during hibernation, as foetuses cannot use lipid as a metabolic substrate and require carbohydrates of maternal gluconeogenic origin (Ramsay & Dunbrack 1986). Birth weight in red deer (*Cervus elaphus*), on the other hand, can be directly correlated to maternal physiological condition, as a function of environmental temperature and food availability, during gestation (Albon *et al.* 1987). In other marine mammals, physiology is known to limit behaviour. The exceptionally slow development of blood and muscle oxygen stores in Australian sea lions (*Neophoca cinerea*) significantly impacts the time by which weaned juveniles can dive aerobically, and the depths they are able to dive to, thus affecting foraging success of young animals (Fowler *et al.* 2007). Harbour seal (*Phoca vitulina*) pups are precocious and can swim and dive at birth (probably supported by high blood oxygen stores), but they are limited from long dives by immature blood oxygen stores (Burns *et al.* 2005).

In contrast, here we have a case in which life history (age of independence) dictates the rate of biochemical development. Further studies on the development of echolocation in odontocetes from both behavioural and physiological perspectives would enhance our understanding of these complex tissues, as would studies at the cellular level aimed at elucidating the mechanisms controlling the fine-scale spatial variation in lipid synthesis and deposition.

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